

Comments on Terms Used in Studies of Speciation Phenomena

by

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At the suggestion of the editor, the following remarks on terminology are offered as a preface to the paper by Harry K. Fritchman on reproductive cycles of central Californian limpets.

ECOLOGIC NICHE. To survive and to reproduce, an animal must satisfy all its essential needs for food, space, shelter, and breeding. At the simplest level, it is this totality of living requirements to which the term "ecologic niche" refers. Thus, niche used in the sense of a physical recess or place especially suiting a given animal species is used wrongly; for niche is not a synonym of habitat. Habitat, as the place where an animal is to be found, is certainly part of its niche, but the idea of niche refers as much to its other needs, or even more so, as will be brought out below.

Next we must say that the idea of niche is meaningless without the implicit recognition of the fact that any animal is associated with other organisms in a grouping characteristic for the given habitat, such as the high wave-washed rocky intertidal. Such a grouping is called a community. The members of this community use the space and the food available there, and presumably they use it so that their densities and their reproductive efforts are adjusted to the usual supplies of this space and food. To a varying degree animals with particular feeding habits, for example, vegetarians such as limpets, will get into each other's way because of similar food requirements. This will especially be true of closely related species such as our West Coast *Acmaeas*, which presumably exploit a lot of the available grazing opportunities. Even more so in their evolutionary histories these species competed for the same feeding opportunities. A great deal of this competition is now relieved by special adaptations in given species to particular segments of the total range within which limpets can graze, but this

does not mean they are cleanly separated in day-to-day life.

These comments now permit us to define "ecologic niche" in a more up-to-date way. A niche is the position of an animal in a community with relation to food and enemies. Now, by animal we of course mean a population that is maintaining itself. This population feeds on something, and other species feed on it. The supply of utilizable food is the most direct determinant of the presence of an animal, and it becomes superfluous to talk about place, or space, or breeding requirements, since these are all implicit in the idea of adequate food supporting the population. There are exceptions to this, but it holds in general and represents a backbone idea in a modern phase of ecology known as production ecology.

Thus, there are at least two ways of defining "niche": (1) As a totality of requirements. This is static. It gets us nowhere; it is a dead end. (2) As a position or occupation filled by an animal in the food-web of a community. This is dynamic. It recognizes the jig-saw puzzle character of a community and sets up an analytical framework for studies such as those of Fritchman.

ECOLOGICAL RANGE. In a community, some animals are restricted to particular places; others seem to range widely within the same community. Without knowing all the factors that set the narrow limits for species in the first group, we refer to them as stenotopic, literally meaning narrow place. To species in the second group we apply the term eurytopic, literally meaning wide place. As was stated above, there are wide grazing opportunities for limpets over most of the rocky intertidal; and the species present there have partitioned this range among themselves through evolution. Some of these segments are larger than average; others are smaller. Hence, eurytopic species and stenotopic species.

SPECIATION. When we have a group of closely related species such as the limpets, we have an opportunity to study factors which may have been critical in their evolution. Speciation is the process of species formation, and in one sense it is the process whereby a way of life or major occupation such as grazing in the rocky intertidal is divided into sub-occupations. In a small town, the supplying job is done by a general store; in a big city, the supplying job is divided according to commodities and then crosswise by the wholesalers, middlemen, and retailers. A natural community is simple or complex according to the same principles of economics. And in some complex communities we get a swarm of closely related species such as limpets whose very presence as so many variations on a basic theme raises intriguing questions. Did these evolve side by side, or did they evolve with long separations in space facilitating their radiation? This brings us to the two kinds of speciation about which students of evolution argue today.

(1) Geographic or allopatric speciation. The term allopatric is applied to distributional ranges of closely related species which complement each other in space; that is, they do not overlap. When this term is used as an adjective modifying speciation, it refers to a particular method of species formation. It is argued that the usual method, and for some students the only method, of speciation consists of the following three steps: first, a geographic separation of a continuous population into two parts; second, the occurrence of differences in the environments of the two populations followed by the divergence of these populations in behavior, physiology, and morphology so that they are respectively better adapted to parts of what was earlier the total environment occupied by the parent species; and third, the breakdown of

the original barrier separating the two populations so that they meet again, but now they do not interbreed and instead behave as distinct species. A barrier which was at first merely geographic is now supplanted by a genetic one, which has evolved as a part of the specializations each of the two populations acquired in their respective ranges while they were separated. This, in brief, is the theory of geographic or allopatric speciation.

(2) In the alternative and less popular method of species formation, by ecologic or sympatric speciation, we have a parent species giving rise to two species without the first condition required by the theory of geographic speciation, that is, without geographic separation. The derivative species co-exist through the period of species formation. The term sympatric means co-existing, and so ecologic or sympatric speciation refers to the formation of two species in one place and the acquisition of genetic isolation between them at some critical point without benefit of the reduction or prevention of interbreeding prior to this point that comes about automatically in geographic speciation. It can be contended, and has been contended, that a swarm of species such as the Acmaea limpets of the central Californian coast could evolve by local separations in time or space so that what was a single interbreeding population is chopped into two at some point because, say, one part likes to live on rocks, the other on snail shells; or because one part breeds in late winter, the other in mid-spring.

In giving us information on reproductive cycles of limpets, Dr. Fritchman addresses himself to this argument about geographic versus ecological speciation. In addition, and what is perhaps more important, he gives us information on the basic ecology of limpets that helps us to understand the impressive radiation that has resulted in this group through evolution.

